© 2017. Published by The Company of Biologists Ltd | Journal of Experimental Biology (2017) 220, 1563-1567 doi:10.1242/jeb.156661

SHORT COMMUNICATION

An evolutionary solution of terrestrial isopods to cope with low atmospheric oxygen levels

Terézia Horváthová*, Andrzej Antoł, Marcin Czarnoleski, Jan Kozłowski and Ulf Bauchinger

ABSTRACT

The evolution of current terrestrial life was founded by major waves of land invasion coinciding with high atmospheric oxygen content. These waves were followed by periods with substantially reduced oxygen concentration and accompanied by the evolution of novel traits. Reproduction and development are limiting factors for evolutionary water–land transitions, and brood care has probably facilitated land invasion. Peracarid crustaceans provide parental care for their offspring by brooding the early stages within the motherly brood pouch, the marsupium. Terrestrial isopod progeny begin ontogenetic development within the marsupium in water, but conclude development within the marsupium in air. Our results for progeny growth until hatching from the marsupium provide evidence for the limiting effects of oxygen concentration and for a potentially adaptive solution. Inclusion of air within the marsupium compensates for initially constrained growth in water through catch-up growth, and it may explain how terrestrial isopods adapted to short- and long-term changes in oxygen concentration.

KEY WORDS: Land invasion, Atmospheric oxygen concentration, Hypoxia, Catch-up growth, Progeny development, Brood care

INTRODUCTION

Atmospheric oxygen concentration is a driving force for many major events in the evolution of life (reviewed in Berner et al., 2007). The origin of metazoan life (Canfield et al., 2007), land invasion by animals (Ward et al., 2006), animal radiation and diversification (Saltzman et al., 2011; Sperling et al., 2013), evolution of modern phytoplankton (Falkowski et al., 2004), placental reproduction (Falkowski et al., 2005), gigantism (Dudley, 1998; Payne et al., 2012) and mass extinction (Huey and Ward, 2005) all represent key evolutionary events closely tied to high, low or rapidly changing oxygen levels on Earth. Many evolutionary innovations such as brood care (Baeza and Fernandez, 2002), metamorphosis (Callier et al., 2013), sexual reproduction (Nevalainen et al., 2011), gas exchange patterns in insects (Lighton and Berrigan, 1995), arrested embryonic development in reptiles (Rafferty and Reina, 2012) and dormancy (Katajisto, 2004) have been put into context with environmental oxygen availability and/or organismal oxygen requirements. These evolutionary strategies may thus either represent adaptations that evolved independently multiple times, in direct response to fluctuating levels of atmospheric oxygen, or alternatively represent secondary adaptations to meet changing oxygen requirements in organisms subject to environmental change.

Here, we show that catch-up growth is probably a further example of such an evolutionary innovation. Switching from aquatic to air conditions during development within the motherly brood pouch of the terrestrial isopod *Porcellio scaber* relaxes oxygen limitations and facilitates accelerated growth under motherly protection. Our findings provide important insights into the role of oxygen in brood care in present-day terrestrial crustaceans.

MATERIALS AND METHODS

Experimental animals

Early development in terrestrial isopods occurs sequentially in aquatic conditions followed by aerial conditions in the motherly brood pouch (Fig. S1; Hoese and Janssen, 1989). Boxes containing gravid females of the terrestrial isopod *Porcellio scaber* Latreille 1804 were maintained in plexi-chambers (40×50×55 cm, YETI-Advertisement Agency, Kryspinów, Poland) with regulated normal (22%) and low oxygen (10%) levels (ROXY-4, Sable Systems Europe GmbH, Berlin, Germany). Plexi-chambers with normoxic and hypoxic conditions were maintained in two climatic chambers with constant temperature of either 15 or 22°C (POL-EKO APARATURA, Sp.j., Wodzisław Śląski, Poland), providing a two-factorial experimental design (15°C and 22% oxygen, 15°C and 10% oxygen, 22°C and 22% oxygen, and 22°C and 10% oxygen). A uniform circulation of air through the closed plexi-chambers was provided by a fan. Relative humidity was regulated to 75% by a separate dew point generator for each of the four plexi-chambers (DG-4, Sable Systems Europe GmbH). The temperature difference of 7°C in our experiment resulted in a twofold increment in oxygen consumption rate (Q_{10}≈2.8) of adult isopods (T.H., unpublished data). Gravid females were examined under a stereomicroscope for the presence/absence of liquid inside the marsupium every 2 days to define the length of the aqueous and gaseous phase (see Fig. S1 for a description of marsupial phases). The current approach is an improvement on our previous study (Horvathova et al., 2015) as it includes a higher time resolution of sampling, determination of the length of both the aqueous and gaseous phases separately, instead of only the total developmental time, and represents a more conservative approach for the determination of the onset of marsupial development. Intramarsupial development is characterized by 20 discrete stages (Milatovič et al., 2010). Because we could not precisely define the first day of gravidity, the length of the aqueous phase was calculated as the time between the appearance of stage 13 (Milatovič et al., 2010) and the day of liquid absorption (see Table S1 for the duration of the first 12 stages). Stage 13 can be easily defined by the presence of hepatopancreatic glands that enclose a conspicuous yolk sac (fig. 1f in Milatovič et al., 2010). The length of the gaseous phase was calculated as the time between the absorption of marsupial

---

Institute of Environmental Sciences, Jagiellonian University, ul. Gronostajowa 7, Kraków 30-387, Poland.

*Author for correspondence (terezia.horvathova@uj.edu.pl)

T.H., 0000-0003-2645-3844

Received 16 January 2017; Accepted 19 February 2017

liquid and the day of hatching. Females were removed and weighed to the nearest 0.01 mg (Mettler Toledo XP26, Greifensee, Switzerland) after hatching. We determined the clutch size and body mass of 10 hatchlings (to the nearest 0.001 mg) for a random subsample of clutches in each condition (see Table 1). Mean hatchling mass was calculated by dividing the total mass by the number of weighed offspring. Mortality of the brood was checked every 2 days and dead females or aborted broods were removed.

Data analysis

All data were tested for normality of distribution and homogeneity of variance prior to analyses. The total number of females used in the analysis was 219. Differences in the total length of brood development, length of the aqueous and gaseous phases, duration of the gaseous phase as a percentage of total development time, clutch size and hatchling body mass were analysed by two-factorial ANCOVA with oxygen and temperature as fixed factors and mother mass as covariate, and all possible interactions were stepwise removed. The interaction term between temperature and oxygen was always retained in the minimum model. Because isopod progeny growth occurs during both the aqueous and gaseous phases (Helden and Hassall, 1998), we analysed this pattern in more detail and tested whether the length of the gaseous phase depends on the length of the aqueous phase. For this analysis, we included the length of the gaseous phase as a dependent variable, temperature and oxygen as fixed factors and the length of the aqueous phase as a covariate, with all possible interactions. The GLIMMIX procedure was used to analyse differences in the survival rates during the aqueous and gaseous phases of brood pouch development. The model included survival as a binary response variable (died/survived during development in the aqueous or gaseous phase), temperature and oxygen as fixed factors and the interaction between these two factors. We did not differentiate between mortality of the brood and mortality of gravid females because females that aborted clutches died within a few days. All statistical analyses were performed with SAS 9.4 statistical software (SAS Institute Inc., Cary, NC, USA).

RESULTS AND DISCUSSION

Oxygen availability determines neither total development time nor hatchling body mass

Our manipulation of oxygen did not affect total development time within the brood pouch (sum of aqueous and gaseous phases; Fig. S1), but total development lasted approximately twice as long in the cold as in the warm (Fig. 1A, Table 1; Fig. S2). Differences in total developmental time did not translate into differences in hatchling body mass; offspring body mass at hatching did not differ significantly between experimental conditions (Table 1). This suggests that development within the marsupium lasts until a predetermined body mass is reached and that ambient temperature – an important driver of growth rate in crustaceans (Hartnoll, 2001; Horvathova et al., 2015) – only determines the time required to reach the predetermined body mass. Because both mortality during development within the brood pouch and mortality during the juvenile stage can reach up to 60–80% in terrestrial isopods (see Table S2; Dangerfield, 1997; Hassall et al., 2005; Zimmer, 2002), females may increase fitness more by increasing hatchling size, rather than increasing fecundity, as increased hatchling body mass will enhance growth and survivorship as a juvenile. This may result in relative constancy of body size, but varying brood size.

Oxygen availability limits development in aqueous phase conditions

With respect to the two constituent phases of marsupial development of present-day terrestrial isopods, we found that oxygen limitations occur during development of the progeny in the aqueous phase but not the gaseous phase within the motherly brood pouch. Under hypoxia, longer development in the initial aqueous conditions in the cold (Fig. 1B, Table 1) was followed by more rapid development in the subsequent gaseous phase at both temperatures (Fig. 1C, Table 1; Fig. S2). Given that oxygen limitation is expected to be greater under warm conditions, this result is of special interest in view of the capacity of brooding *P. scaber* females to supply oxygen to embryos under varying temperature conditions. Female isopods actively provide oxygen to their progeny only during the aqueous phase, through special structures called cotyledons within the marsupial cavity (Hoese and Janssen, 1989) that have evolved as a novel adaptation to terrestrial habitats (Csonka et al., 2013; Hornung, 2011). Females under conditions of low environmental oxygen and temperature may be limited in the supply of oxygen as a result of their slow metabolic rate and increased oxygen demand of the brood, and this might explain why progeny spent a proportionally longer time in the aqueous phase. Longer development in the aqueous phase may be necessary to achieve a state of development in preparation for subsequent development in gaseous conditions. This result suggests that the limits to oxygen

Table 1. Effects of temperature (15 and 22°C) and oxygen level (10% and 22%) on brood life-history characteristics of terrestrial isopod *Porcellio scaber*

	22% oxygen		10% oxygen			*F*-value, *P*-value			
	22°C	15°C	22°C	15°C	d.f.	O_2	Temp.	Temp.× O_2	Mother mass
Clutch size	40±11.4 (11)	45±5.5 (4)	41±6.6 (8)	32±6.0 (5)	4,27	0.67 0.423	0.29 0.6	1.76 0.197	13.84 **0.001**
Hatchling mass (mg)	0.48±0.1 (11)	0.48±0.1 (6)	0.46±0.1 (8)	0.46±0.1 (5)	4,27	1.46 0.239	0.03 0.872	0.05 0.818	1.06 0.314
Total time (days)	15±1.3 (30)	29±4.0 (16)	14±1.7 (42)	31±3.1 (13)	4,90	0.02 0.88	807.76 **<0.0001**	3.18 0.078	0.51 0.478
Aqueous phase (days)	10±1.1 (36)	20±3.9 (16)	10±1.4 (49)	22±3.2 (15)	4,98	3.72 0.057	512.77 **<0.0001**	4.11 **0.045**	0.01 0.937
Gaseous phase (days)	5±0.9 (33)	9±1.2 (16)	4.5±1.3 (51)	8±2.7 (13)	4,102	5.46 **0.021**	142.11 **<0.0001**	0.08 0.783	0.83 0.364
Gaseous phase (% total)	33±4.7 (30)	32±5.1 (16)	31±8.4 (42)	27±8.2 (13)	4,90	4.22 **0.043**	1.34 0.249	0.63 0.429	0.92 0.341

Data under different oxygen–temperature conditions are given as means±s.d., with sample size in parentheses. Mother mass was used in a final model as a covariate. Statistically significant *P*-values are in bold. Main effects are reported from the model, excluding non-significant interactions.

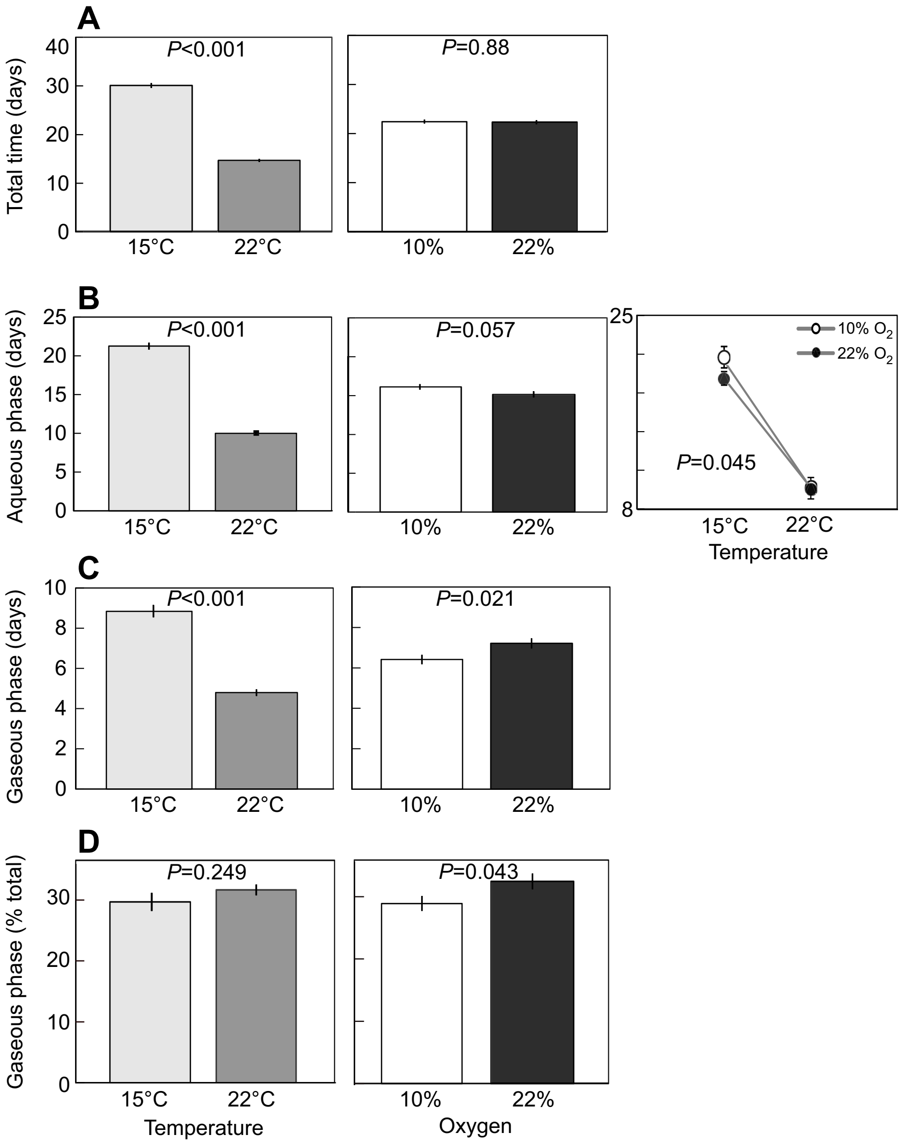

Fig. 1. Effects of temperature (15 and 22°C) and oxygen level (10% and 22%) on developmental phases within the motherly brood pouch of the terrestrial isopod *Porcellio scaber*. (A) Total developmental time was affected by temperature but not oxygen level. (B) Length of the aqueous phase was affected by temperature and oxygen, but the effect of oxygen was apparent only under low-temperature conditions. (C) Length of the gaseous phase was shorter under conditions of warm temperature and low oxygen. (D) Gaseous phase as a percentage of the total length of brood pouch development was affected by oxygen but not temperature. Data show least-square means±s.e.

supply imposed by the environmental conditions may restrict the mother's capacity to provide adequate oxygen to the brood.

Oxygen availability determines the duration of the gaseous phase as a percentage of total development time

The total developmental time of the progeny was not affected by oxygen levels; however, the relative distribution of time spent in the aqueous and air phases differed significantly (Fig. 1D, Table 1; Fig. S2). Progeny developing under 22% oxygen and thus less constrained by oxygen availability during the initial aqueous phase spent a proportionally longer time developing in the subsequent gaseous phase compared with progeny developing in 10% oxygen (Fig. 1D). Because the same hatchling size was attained, we infer that processes that govern completion of intramarsupial development might be differentially affected by oxygen availability during the two marsupial phases; any effect during the aquatic phase may be compensated for during the gaseous phase. At present, we can only speculate about potential constraints leading to the ratio between the two phases, such as growth and development of the digestive system, cuticular protuberances or the tubular heart (Milatovič et al., 2010; Mrak et al., 2014; Štrus et al., 2008; Wolff, 2009).

Oxygen limitations are relaxed in air conditions

We interpret our results for the two-factorial experimental design with low and normal oxygen levels and high and low ambient temperature levels to provide an example of catch-up growth (Metcalfe and Monaghan, 2001). Our analysis on differences in developmental timing within individual broods showed that offspring that were subjected to a period of constrained development in the aqueous phase under 10% oxygen shortened development time in the gaseous phase (aqueous phase×oxygen: $F_{5,103}$=4.48, P=0.037; Fig. 2) and attained a final size not different from that of non-constrained individuals under 22% oxygen (Table 1). These results are in agreement with the physical properties of oxygen in water and air, with oxygen being 20- to 40-fold more abundant and diffusing 10,000 times more rapidly in air than in water (Denny, 1993). Constrained growth in water may be attributed to the brooding costs of oxygen provisioning by the mother (Fernández et al., 2000), which can be later offset by increased oxygen availability in air. Growing in sheltered conditions under motherly protection but completing intramarsupial development under relaxed oxygen constraints – through the incorporation of a gaseous phase – may thus represent an important evolutionary strategy for life under transient hypoxic environments.

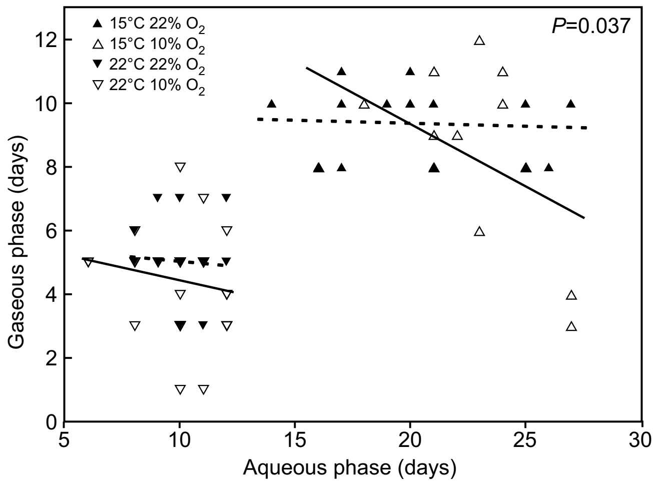

Fig. 2. Association between the length of the aqueous phase and the length of the gaseous phase of brood pouch development under different temperature (15 and 22°C) and oxygen (10% and 22%) conditions in the terrestrial isopod *P. scaber*. The significant interaction between the length of the aqueous phase and oxygen levels exemplifies catch-up growth. Individuals with constrained development in the aqueous phase under 10% oxygen shortened the duration of growth in the gaseous phase and hatched at a body size not different from that of non-constrained individuals (Table 1). The points represent values for single mothers. Regression lines for low and normal oxygen conditions are represented by solid and dashed lines, respectively.

Catch-up growth as an evolutionary strategy

Catch-up growth represents an evolutionary strategy that compensates for a poor start in an animal's life, such that: 'animals that have experienced a period of retarded growth […] then enter a phase of growth acceleration when conditions improve' (Metcalfe and Monaghan, 2001). Catch-up growth is a widely used strategy among vertebrates and invertebrates and it commonly occurs under conditions of nutritional deficit (Dmitriew and Rowe, 2007; Hector and Nakagawa, 2012; Malzahn and Boersma, 2012; Morgan and Metcalfe, 2001), but accelerated growth is also seen in response to environmental cues (De Block and Stoks, 2008; Orizaola et al., 2014). Here, we provide evidence for catch-up growth during early development within the motherly brood pouch of terrestrial isopods, which we believe to be the first report regarding catch-up growth in conjunction with oxygen availability. In the present case, low environmental oxygen concentration initially increased development duration and was subsequently compensated through catch-up growth after the oxygen limitation was relaxed.

Colonization of land appeared in two major waves, each corresponding with high atmospheric oxygen content: the first invasion occurred between 425 and 360 million years ago (Mya) and was followed by a second one beginning approximately 345 Mya (Berner et al., 2007; Ward et al., 2006). Isopods – the most successful terrestrial colonizers among crustaceans (>3600 species; Schmalfuss, 2003) – invaded land during the second major wave (Broly et al., 2013, 2015), when atmospheric oxygen content reached its maximum value (Fig. 3), indicating relaxed conditions for processes with high oxygen demands. A brood pouch as a brooding strategy of crustaceans evolved long before, as indicated by fossil records of marsupia (Fig. 3; Broly et al., 2017; Siveter et al., 2014). It has been suggested that animals that evolved under such high oxygen levels and then survived the mass extinction during the subsequent period of low oxygen content (Fig. 3) underwent major modifications of their body plans (Huey and Ward, 2005; Payne et al., 2013; Ward, 2006). We hypothesize that oxygen may have played an important role in the evolution of brood care in isopods (Fig. 3). While in a marine environment, a brood pouch may have primarily protected eggs from mechanical damage (Steele, 1991), it may have progressively evolved into a more complex structure with a supply of water (Carefoot and Taylor, 1995) and oxygen (Hoese and Janssen, 1989) and the inclusion of a gaseous phase at a later stage of development (this study). Concluding development within the motherly brood pouch in air by implementing gaseous conditions may have relaxed the constraints imposed by the female's limited capacity to supply oxygen and may also have enabled progeny to respond to hypoxic conditions via catch-up growth as a key innovation for life on land. We hypothesize that spatial and temporal variation in oxygen availability may possibly result in strong selective forces promoting the evolution of novel traits.

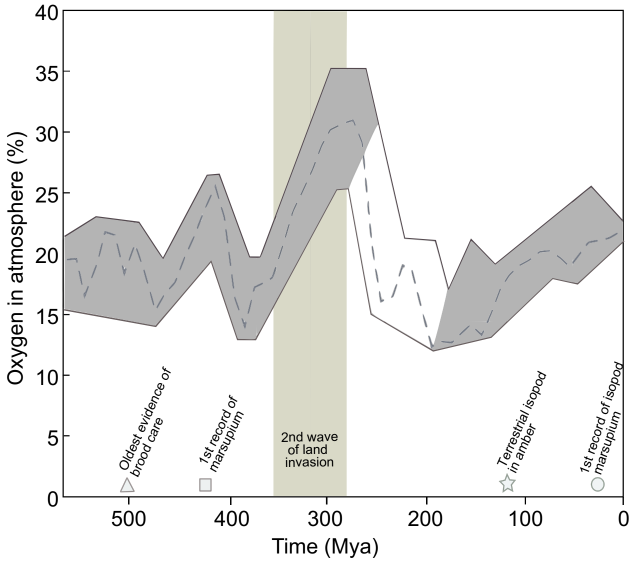

Fig. 3. Changes in atmospheric oxygen concentration during the history of life as a likely driver for the evolution of brood care in crustaceans. Average oxygen values and confidence intervals were extracted from Berner et al. (2007). The emergence of brood care in early arthropods is evidenced by *in situ* eggs with preserved embryos in the fossil record dated to 508 Mya (triangle; Caron and Vannier, 2016). The fossil record of the marsupium of ostracod species signifies egg-brooding as a reproductive strategy in crustaceans approximately 425 Mya in a marine environment (square; Siveter et al., 2007). Isopods invaded land approximately 300 Mya, coinciding with a hyperoxygenated atmosphere (gray band). The subsequent period was characterized by a steep decline in oxygen content by more than half (striped area; Huey and Ward, 2005), which might have selected for body plan innovations such as the inclusion of air within the brood pouch. The period between the invasion of land and the earliest evidence of brooding terrestrial isopods (star and circle; Broly et al., 2013, 2015, 2017) suggests that changing atmospheric oxygen concentrations might have promoted novel adaptations for life on land. Time is given as means and 95% confidence intervals.

Acknowledgements
We thank Edyta Sadowska, Maciej Pabijan, Aleksandra Walczyńska and Manfred Bauchinger for critical comments. We thank the two anonymous reviewers for their valuable comments on the manuscript.

Competing interests
The authors declare no competing or financial interests.

Author contributions
T.H. and A.A. performed the experiment. T.H., M.C., J.K. and U.B. designed the experiment. T.H. and U.B. wrote the manuscript with input from A.A., J.K. and M.C.

Funding

This research was funded by a MAESTRO grant from Narodowe Centrum Nauki (2011/02/A/NZ8/00064).

Data availability

Data are archived in figshare: https://dx.doi.org/10.6084/m9.figshare.3491423.v2.

Supplementary information

Supplementary information available online at
http://jeb.biologists.org/lookup/doi/10.1242/jeb.156661.supplemental

References

Baeza, J. A. and Fernandez, M. (2002). Active brood care in Cancer setosus (Crustacea: Decapoda): the relationship between female behaviour, embryo oxygen consumption and the cost of brooding. *Funct. Ecol.* **16**, 241-251.

Berner, R. A., VandenBrooks, J. M. and Ward, P. D. (2007). Oxygen and evolution. *Science* **316**, 557-558.

Broly, P., Deville, P. and Maillet, S. (2013). The origin of terrestrial isopods (Crustacea: Isopoda: Oniscidea). *Evol. Ecol.* **27**, 461-476.

Broly, P., Maillet, S. and Ross, A. J. (2015). The first terrestrial isopod (Crustacea: Isopoda: Oniscidea) from Cretaceous Burmese amber of Myanmar. *Cretaceous Res.* **55**, 220-228.

Broly, P., Serrano-Sánchez, M. d. L., Rodríguez-García, S. Vega, F. J. (2017). Fossil evidence of extended brood care in new Miocene Peracarida (Crustacea) from Mexico. *J. Syst. Palaeontol.* 1-13.

Callier, V., Shingleton, A. W., Brent, C. S., Ghosh, S. M., Kim, J. and Harrison, J. F. (2013). The role of reduced oxygen in the developmental physiology of growth and metamorphosis initiation in Drosophila melanogaster. *J. Exp. Biol.* **216**, 4334-4340.

Canfield, D. E., Poulton, S. W. and Narbonne, G. M. (2007). Late-Neoproterozoic deep-ocean oxygenation and the rise of animal life. *Science* **315**, 92-95.

Carefoot, T. H. and Taylor, B. E. (1995). Ligia: A prototypal terrestrial isopod. In *Crustacean issues 9: Terrestrial Isopod Biology* (ed. M. A. Alikhan), pp. 47-60. Rotterdam: Balkema.

Caron, J.-B. and Vannier, J. (2016). Waptia and the diversification of brood care in early arthropods. *Curr. Biol.* **26**, 69-74.

Csonka, D., Halasy, K., Szabó, P., Mrak, P., Štrus, J. and Hornung, E. (2013). Eco-morphological studies on pleopodal lungs and cuticle in Armadillidium species (Crustacea, Isopoda, Oniscidea). *Arthropod. Struct. Dev.* **42**, 229-235.

Dangerfield, J. M. (1997). Growth and survivorship in juvenile woodlice: Is birth mass important? *Ecography* **20**, 132-136.

De Block, M. and Stoks, R. (2008). Compensatory growth and oxidative stress in a damselfly. *Proc. R. Soc. Lond. B Biol. Sci.* **275**, 781-785.

Denny, M. W. (1993). *Air and Water: the Biology and Physics of Life's Media*. Princeton, N.J: Princeton University Press.

Dmitriew, C. and Rowe, L. (2007). Effects of early resource limitation and compensatory growth on lifetime fitness in the ladybird beetle (Harmonia axyridis). *J. Evol. Biol.* **20**, 1298-1310.

Dudley, R. (1998). Atmospheric oxygen, giant Paleozoic insects and the evolution of aerial locomotor performance. *J. Exp. Biol.* **201**, 1043-1050.

Falkowski, P. G., Katz, M. E., Knoll, A. H., Quigg, A., Raven, J. A., Schofield, O. and Taylor, F. J. R. (2004). The evolution of modern eukaryotic phytoplankton. *Science* **305**, 354-360.

Falkowski, P. G., Katz, M. E., Milligan, A. J., Fennel, K., Cramer, B. S., Aubry, M. P., Berner, R. A., Novacek, M. J. and Zapol, W. M. (2005). The rise of oxygen over the past 205 million years and the evolution of large placental mammals. *Science* **309**, 2202-2204.

Fernández, M., Bock, C. and Pörtner, H.-O. (2000). The cost of being a caring mother: the ignored factor in the reproduction of marine invertebrates. *Ecol. Lett.* **3**, 487-494.

Hartnoll, R. G. (2001). Growth in Crustacea-twenty years on. *Hydrobiologia* **449**, 111-122.

Hassall, M., Helden, A., Goldson, A. and Grant, A. (2005). Ecotypic differentiation and phenotypic plasticity in reproductive traits of Armadillidium vulgare (Isopoda: Oniscidea). *Oecologia* **143**, 51-60.

Hector, K. L. and Nakagawa, S. (2012). Quantitative analysis of compensatory and catch-up growth in diverse taxa. *J. Anim. Ecol.* **81**, 583-593.

Helden, A. J. and Hassall, M. (1998). Phenotypic plasticity in growth and development rates of Armadillidium vulgare (Isopoda: Oniscidea). *Israel J. Zool.* **44**, 379-394.

Hoese, B. and Janssen, H. H. (1989). Morphological and physiological-studies on the marsupium in terrestrial isopods. *Monit. Zool. Ital. N.S. Monografia* **4**, 153-173.

Hornung, E. (2011). Evolutionary adaptation of oniscidean isopods to terrestrial life: structure, physiology and behavior. *Terr. Arthropod Rev.* **4**, 95-130.

Horvathova, T., Antol, A., Czarnoleski, M., Kramarz, P., Bauchinger, U., Labecka, A. M. and Kozlowski, J. (2015). Does temperature and oxygen affect duration of intramarsupial development and juvenile growth in the terrestrial isopod Porcellio scaber (Crustacea, Malacostraca)? *Zookeys* 67-79.

Huey, R. B. and Ward, P. D. (2005). Hypoxia, global warming, and terrestrial Late Permian extinctions. *Science* **308**, 398-401.

Katajisto, T. (2004). Effects of anoxia and hypoxia on the dormancy and survival of subitaneous eggs of Acartia bifilosa (Copepoda: Calanoida). *Mar. Biol.* **145**, 751-757.

Lighton, J. R. B. and Berrigan, D. (1995). Questioning paradigms-caste-specific ventilation in harvester ants, Messor pergandei and M. julianus (Hymenoptera, Formicidae). *J. Exp. Biol.* **198**, 521-530.

Malzahn, A. M. and Boersma, M. (2012). Effects of poor food quality on copepod growth are dose dependent and non-reversible. *Oikos* **121**, 1408-1416.

Metcalfe, N. B. and Monaghan, P. (2001). Compensation for a bad start: grow now, pay later? *Trends Ecol. Evol.* **16**, 254-260.

Milatovič, M., Kostanjšek, R. and Štrus, J. (2010). Ontogenetic development of Porcellio scaber: staging based on microscopic anatomy. *J. Crustacean Biol.* **30**, 225-235.

Morgan, I. J. and Metcalfe, N. B. (2001). Deferred costs of compensatory growth after autumnal food shortage in juvenile salmon. *Proc. R. Soc. Lond. B Biol. Sci.* **268**, 295-301.

Mrak, P., Žnidaršič, N., Žagar, K., Čeh, M. and Štrus, J. (2014). Exoskeletal cuticle differentiation during intramarsupial development of Porcellio scaber (Crustacea: Isopoda). *Arthropod Struct. Dev.* **43**, 423-439.

Nevalainen, L., Sarmaja-Korjonen, K., Luoto, T. P. and Kultti, S. (2011). Does oxygen availability regulate sexual reproduction in local populations of the littoral cladoceran Alonella nana? *Hydrobiologia* **661**, 463-468.

Orizaola, G., Dahl, E. and Laurila, A. (2014). Compensatory growth strategies are affected by the strength of environmental time constraints in anuran larvae. *Oecologia* **174**, 131-137.

Payne, J. L., Groves, J. R., Jost, A. B., Nquyen, T., Moffitt, S. E., Hill, T. M. and Skotheim, J. M. (2012). Late paleozoic fusulinoidean gigantism driven by atmospheric hyperoxia. *Evolution* **66**, 2929-2939.

Payne, J. L., Jost, A. B., Wang, S. C. and Skotheim, J. M. (2013). A shift in the long-term mode of foraminiferan size evolution caused by the end-Permian mass extinction. *Evolution* **67**, 816-827.

Rafferty, A. R. and Reina, R. D. (2012). Arrested embryonic development: a review of strategies to delay hatching in egg-laying reptiles. *Proc. R. Soc. Lond. B Biol. Sci.* **279**, 2299-2308.

Saltzman, M. R., Young, S. A., Kump, L. R., Gill, B. C., Lyons, T. W. and Runnegar, B. (2011). Pulse of atmospheric oxygen during the late Cambrian. *Proc. Natl. Acad. Sci. USA* **108**, 3876-3881.

Schmalfuss, H. (2003). World catalog of terrestrial isopods (Isopoda: Oniscidea). *Stuttgarter Beiträge zur Naturkunde Serie A Nr.* **654**, 341.

Siveter, D. J., Siveter, D. J., Sutton, M. D. and Briggs, D. E. G. (2007). Brood care in a Silurian ostracod. *Proc. R. Soc. Lond. B Biol. Sci.* **274**, 465-469.

Siveter, D. J., Tanaka, G., Farrell, U. C., Martin, M. J., Siveter, D. J. and Briggs, D. E. G. (2014). Exceptionally preserved 450-million-year-old ordovician ostracods with brood care. *Curr. Biol.* **24**, 801-806.

Sperling, E. A., Frieder, C. A., Raman, A. V., Girguis, P. R., Levin, L. A. and Knoll, A. H. (2013). Oxygen, ecology, and the Cambrian radiation of animals. *Proc. Natl. Acad. Sci. USA* **110**, 13446-13451.

Steele, D. H. (1991). Is the oostegite structure of amphipods determined by their phylogeny or is it an adaptation to their environment? *Hydrobiologia* **223**, 27-34.

Štrus, J., Klepal, W., Repina, J., Tušek-Žnidarič, M., Milatovič, M. and Pipan, Z. (2008). Ultrastructure of the digestive system and the fate of midgut during embryonic development in Porcellio scaber (Crustacea: Isopoda). *Arthropod Struct. Dev.* **37**, 287-298.

Ward, D. P. (2006). *Dinosaurs, Birds, and Earth's Ancient Atmosphere-Out of Thin Air*, pp. 282. Washington, D.C: Joseph Henry Press.

Ward, P., Labandeira, C., Laurin, M. and Berner, R. A. (2006). Confirmation of Romer's Gap as a low oxygen interval constraining the timing of initial arthropod and vertebrate terrestrialization. *Proc. Natl. Acad. Sci. USA* **103**, 16818-16822.

Wolff, C. (2009). The embryonic development of the malacostracan crustacean Porcellio scaber (Isopoda, Oniscidea). *Dev. Genes Evol.* **219**, 545-564.

Zimmer, M. (2002). Postembryonic ontogenetic development in Porcellio scaber (Isopoda: Oniscidea): the significance of food. *Invertebr. Repr. Dev.* **42**, 75-82.